

# Impulsive Choice and Altruistic Punishment Are Correlated and Increase in Tandem With Serotonin Depletion

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Human cooperation may partly depend on the presence of individuals willing to incur personal costs to punish noncooperators. The psychological factors that motivate such ‘altruistic punishment’ are not fully understood; some have argued that altruistic punishment is a deliberate act of norm enforcement that requires self-control, while others claim that it is an impulsive act driven primarily by emotion. In the current study, we addressed this question by examining the relationship between impulsive choice and altruistic punishment in the ultimatum game. As the neurotransmitter serotonin has been implicated in both impulsive choice and altruistic punishment, we investigated the effects of manipulating serotonin on both measures. Across individuals, impulsive choice and altruistic punishment were correlated and increased following serotonin depletion. These findings imply that altruistic punishment reflects the absence rather than the presence of self control, and suggest that impulsive choice and altruistic punishment share common neural mechanisms.

*Keywords:* altruistic punishment, decision-making, self-control, impulsivity, serotonin

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Unlike most other species, humans cooperate in large groups, with strangers they are unlikely to encounter again, and often in the absence of immediate external reinforcement. Recent work in economics and evolutionary biology suggests that these aspects of human cooperation are driven in part by the presence of individuals willing to incur personal costs to punish noncooperators (Fehr & Gächter, 2002). Such ‘altruistic punishment’ has been observed across diverse human societies (Henrich et al., 2006) and poses a puzzle: why do people punish noncooperators despite the fact that such actions are personally costly?

The psychological root of altruistic punishment has been debated. Some have suggested that altruistic punishment is a delib-

erate act of social norm enforcement that requires self-control (Knoch & Fehr, 2007; Knoch, Pascual-Leone, Meyer, Treyer, & Fehr, 2006). Others claim the opposite: that altruistic punishment is an impulsive act driven primarily by emotional reactions to perceived unfairness (Koenigs & Tranel, 2007; Pillutla & Murnighan, 1996; Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003; Tabibnia, Satpute, & Lieberman, 2008). In the current study, we address this question by directly examining whether altruistic punishment behavior correlates positively or negatively with impulsive choice, an independent measure of self-control in the context of decision-making. In addition, we examined whether impulsive choice and altruistic punishment were modulated in similar or different ways by changes in serotonin, a neurotransmitter implicated both in self-control and social decision-making.

We measured altruistic punishment behavior using the Ultimatum Game (UG). In this game, two players must agree to share a sum of money, or neither player gets any money. One player, the proposer, suggests a way to split the sum. The other player, the responder, either accepts the offer and both players are paid accordingly, or rejects the offer and neither player is paid. Despite the fact that rejecting an offer means forfeiting payment, responders tend to punish proposers who violate fairness norms by rejecting their unfair offers (usually less than 20 to 30% of the total stake) (Guth, Schmittberger, & Schwartz, 1982). Thus, rejecting unfair offers in the UG is an example of “costly” or “altruistic” punishment. Note that the “cost” of punishment refers to the potential earning that the responder could have otherwise earned.

Proponents of the self-control account of altruistic punishment behavior argue that responders in the UG are tempted to selfishly

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accept all offers and must exercise self-control to enforce fairness goals and reject unfair offers. Evidence from neuroeconomics has implicated the dorsolateral prefrontal cortex (DLPFC), a brain region implicated in self-control (Miller & Cohen, 2001), in the implementation of these fairness goals. The DLPFC is activated when responders decide whether to reject unfair offers in the UG (Sanfey et al., 2003), and disrupting DLPFC activity with transcranial magnetic stimulation reduces rejection of unfair offers, suggesting that the DLPFC normally promotes rejection of unfair offers (Knoch et al., 2006).

In contrast, supporters of the emotional hypothesis of altruistic punishment behavior point out that self-reported anger predicts whether individuals reject unfair offers in the UG (Pillutla & Murnighan, 1996), and inducing negative affect increases the rate of rejection of unfair offers (Harle & Sanfey, 2007). Moreover, increased physiological arousal in response to unfair offers in the UG magnifies the likelihood of rejection (van't Wout, Kahn, Sanfey, & Aleman, 2006), as does activity in the insula (Sanfey et al., 2003; Tabibnia et al., 2008), a brain region linked to negative emotional states (Calder, Lawrence, & Young, 2001). In the context of the UG, these emotional reactions to unfair offers result in monetary loss. Avoiding these losses involves "swallowing one's pride" and accepting unfair offers, foregoing the opportunity to punish unfair proposers by rejecting their offers. Self-control, rather than facilitating altruistic punishment, may instead be employed to promote long-term material self-interest by overriding the emotional impulse to punish. Supporting this view, two recent studies reported greater activity in the right ventrolateral prefrontal cortex (VLPFC), another brain region implicated in self-control (Aron, Robbins, & Poldrack, 2004; Cohen & Lieberman, in press), when participants accept unfair offers in the UG (Halko, Hlushchuk, Hari, & Schurmann, 2009; Tabibnia et al., 2008). Increased activity in right VLPFC during acceptance of unfair offers was associated with reduced activity in the insula, suggesting that the decision to forego altruistic punishment may involve down-regulating the negative emotional response to unfair treatment (Tabibnia et al., 2008). According to this view, then, succumbing to the desire to engage in altruistic punishment represents a breakdown of self-regulation.

Because activity in brain regions associated with self-control has been observed both during the decision to engage in altruistic punishment (Sanfey et al., 2003) and the decision to refrain from it (Halko et al., 2009; Tabibnia et al., 2008), these studies cannot resolve the question of whether altruistic punishment in the UG reflects the presence or absence of self-control; and no behavioral study has directly examined whether altruistic punishment reflects the presence or absence of self-control. The first aim of the current study was to examine whether individual differences in self-control in the context of decision-making, assessed using a well-validated measure of impulsive choice, were related to individual differences in the tendency to engage in altruistic punishment.

We measured individual differences in impulsive choice using the delay-discounting task (Kirby, Petry, & Bickel, 1999), in which subjects make a series of choices between a small reward available immediately, and a larger reward available after a delay. Individuals who prefer small immediate rewards on this measure (i.e., choose impulsively) are more likely to suffer from disorders of self-control in the real world, such as drug addiction, obesity, and pathological gambling (Bickel et al., 2007; Petry, 2001; Reynolds, 2006; Weller, Cook, Avsar, & Cox, 2008). Research in

behavioral neuroscience (Evenden, 1999; Winstanley et al., 2004) and psychology (Kirby & Finch, 2010; Patton et al., 1995; Reynolds et al., 2006) indicates that impulsivity is a complex construct with many facets or 'varieties', including impulsive choice (inability to wait), motor impulsivity (favoring speed over accuracy), and attentional impulsivity (high distractibility), among others, with similarly distinct neural and neurochemical substrates. For the current study, we chose to focus specifically on impulsive choice because of its external ecological validity as a measure of self-control (Bickel et al., 2007; Petry, 2001; Reynolds, 2006; Weller, Cook, Avsar, & Cox, 2008) and its clear relevance in the context of decision-making (Kirby & Finch, 2010; Reynolds et al., 2006). A recent hierarchical component analysis of impulsivity in fact found that performance on the discounting task correlated with multiple components of impulsivity (Kirby & Finch, 2010).

To examine whether altruistic punishment in the UG reflects the presence or absence of self-control, we correlated individual differences in impulsive choice on the delay-discounting task with individual differences in altruistic punishment in the UG. If altruistic punishment requires self-control, these measures should be negatively correlated; if altruistic punishment reflects emotional reactions to perceived unfairness, these measures should be positively correlated.

As a second test of whether altruistic punishment in the UG is an act of self-control, we observed the effects of manipulating the neurotransmitter serotonin on both altruistic punishment in the UG and impulsive choice in the delay-discounting task. Serotonin has been suggested to promote self-control in general (Carver, Johnson, & Joermann, 2008), and disrupting serotonin function reduces self-control on a variety of measures, including delay-discounting (Mobini et al., 2000; Schweighofer et al., 2008). Showing that impulsive choice and altruistic punishment are not only correlated, but similarly influenced in tandem by serotonin, would provide even stronger evidence that these two measures capture common psychological processes.

Twenty-two healthy volunteers attended two experimental sessions, at least 1 week apart. In one session, they underwent acute tryptophan depletion, a procedure that temporarily lowers brain serotonin levels by limiting the availability of tryptophan, the amino acid precursor to serotonin (Carpenter et al., 1998; Cooper, Bloom, & Roth, 2003). In the other session, they received a placebo treatment that did not alter serotonin levels. On each visit, participants completed the delay-discounting task and played the role of responder in the UG. We previously reported that lowering serotonin in this sample increased altruistic punishment in the UG (Crockett et al., 2008). In line with previous findings (Schweighofer et al., 2008), we predicted that lowering serotonin would increase impulsive choice on the delay-discounting task, and that changes in impulsive choice induced by tryptophan depletion would correlate with changes in altruistic punishment induced by tryptophan depletion.

## Method

### Participants

Twenty-two healthy volunteers (7 men, mean age = 25.7) participated. Blood samples were unavailable for two subjects. Exclusion criteria included history of cardiac, hepatic, renal, pul-

monary, neurological, psychiatric or gastrointestinal disorders, medication/drug use, and personal or family history of major depression or bipolar affective disorder. Participants were financially compensated for participating. Additional data collected in this sample have been reported elsewhere (Crockett et al., 2008; Crockett, Clark, & Robbins, 2009).

### Tryptophan Depletion Procedure

Participants were assigned to receive either the tryptophan depleting drink or the placebo mixture on the first session in a double-blind, approximately counterbalanced order. In the tryptophan depletion procedure, tryptophan was depleted by ingestion of a liquid amino acid load that did not contain tryptophan but did include other large neutral amino acids (LNAA); the placebo mixture was identical to the tryptophan depletion mixture, except it contained 3g of tryptophan. Details of the procedure have been described previously (Crockett et al., 2008). To obtain a continuous measure of tryptophan depletion across subjects, we calculated the change, from baseline to pretest, in the ratio of tryptophan to other large neutral amino acids (TRP: $\Sigma$ LNAA ratio) in the plasma. Reduction of the TRP: $\Sigma$ LNAA ratio is a proxy index of tryptophan depletion in the brain, because tryptophan competes with other large neutral amino acids for transport across the blood–brain barrier. The tryptophan depletion procedure caused significant decreases in the TRP: $\Sigma$ LNAA ratios, averaging 85%.

### The Ultimatum Game

Participants played 48 one-shot UGs via computer interface. To enhance the credibility of the UG task, participants were told that they were part of a large ongoing study in which they would be playing the role of responder with volunteers who had submitted their offers previously. In addition, they were told they would have the opportunity to play the role of proposer with volunteers who would participate in the future, if they would allow their photograph to be taken and used in future sessions, and submit proposals for 12 different stake sizes. Four participants declined having their photograph taken. In reality, there were no actual proposers, and participants' proposals were not used beyond their function as a cover story. Before the game started, the experimenter required a verbal confirmation that the participant understood the game. Participants were told that they would receive the financial outcomes from two trials that would be randomly selected at the end of the game. During each trial, participants viewed sequentially a photograph of the proposer (1,500 ms), the amount of the stake (total pie to be shared) (1,500 ms), and the amount of the offer (3,000 ms). Participants responded to each offer by pressing one of two buttons (labeled "accept" and "reject") while the offer was on the screen. On each session, participants played 48 games, each with a different proposer. Proposer identities were randomly matched with offers. There were 8 fair offers, ranging from 40–50% of the stake; 8 medium offers, ranging from 27–33% of the stake; and 8 unfair offers, ranging from 18–22% of the stake, each presented twice. Participants received identical offers at each session, but the order of offers was randomized to disguise this. On different trials, the same monetary amount could appear as a large percentage of the total stake and therefore "fair," or as a small percentage of the total stake and therefore "unfair." This design

allowed us to observe independent effects of tryptophan depletion on responding to different levels of fairness versus different levels of monetary reward. The critical dependent measures were the proportions of offers rejected at each level of fairness and at each level of monetary reward. The main effects of offer size and offer fairness on rejection rates in this sample are reported elsewhere (Crockett et al., 2008).

### Delay Discounting Task

The task consisted of 31 hypothetical choices between "£*m* today" and "£*m'* in *d* days," where  $m < m'$ , *m* ranged from 11 to 80, *m'* ranged from 25 to 85, and *d* ranged from 7 to 186. Subjects were instructed to indicate which option they would prefer. The first 4 choices were practice trials and excluded from the analysis. Choice data for each subject were fit to a hyperbolic discount function using the procedure described in Kirby, Petry, and Bickel (1999). The dependent measure of interest was the discount parameter *k*, or steepness of the hyperbolic discount function. The task yielded three separate values of *k*, for small (£25–35), medium (£50–60), and large (£75–85) rewards. To examine the relationship between delay discounting and altruistic punishment, we used the average *k* value (mean of small, medium, and large *k* values). Larger values of *k* denote stronger preference for small immediate rewards over larger delayed rewards (i.e., impulsive choice). Raw discount parameters were natural log transformed before analysis.

### General Procedure

Participants completed two separate sessions, separated by at least 1 week, and were asked to abstain from food, alcohol, and caffeine from midnight before each session. Upon arrival between 8 and 10:30 am, participants completed a mood rating questionnaire, gave a blood sample, and ingested either the placebo or the tryptophan-depleting amino acid drink. After a resting period of ~5.5 hr, participants completed a second mood rating questionnaire, gave a second blood sample, and completed the test battery, which included the UG and the temporal discounting task. Self-report mood was assessed at three other time points during the battery. Tryptophan depletion did not reliably affect mood, as described previously (Crockett et al., 2008).

## Results

### Impulsive Choice Is Positively Correlated With Altruistic Punishment in the Ultimatum Game

To test whether individual differences in impulsive choice were related to individual differences in altruistic punishment, we correlated performance on the delay-discounting task (collapsed across session and reward size) with rejection rates of fair, medium and unfair offers in the UG (collapsed across session). Across subjects, impulsive choice was positively correlated with rejection rates of unfair offers ( $r = .482, p = .023$ ; Figure 1), but not medium offers ( $r = .212, p = .313$ ) or fair offers ( $r = .060, p = .791$ ). In other words, individuals who preferred smaller immediate rewards to larger delayed rewards were more likely to reject unfair offers in the UG. This relationship held for both the placebo

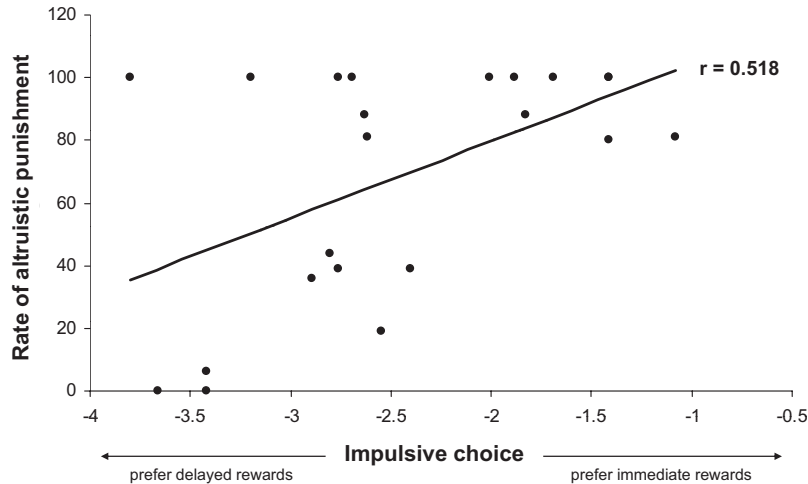


Figure 1. Collapsed across session, impulsive choice on the delay discounting task (log-transformed discount parameter) was significantly and positively correlated with costly punishment in the UG (percent of unfair offers rejected),  $r = 0.518$ ,  $p = 0.023$ .

session and the tryptophan depletion session (see supplementary results).

### Lowering Serotonin Increases Impulsive Choice in Delay-Discounting

We next tested the effect of tryptophan depletion on delay-discounting of small, medium and large rewards. We conducted a repeated-measures ANOVA with treatment and reward size as within-subjects factors, and degree of biochemical tryptophan depletion (the TRP: $\Sigma$ LNAA ratio) as a covariate. This analysis revealed a marginally significant main effect of treatment ( $F(1, 18) = 4.264$ ,  $p = .054$ ,  $\eta_p^2 = 0.192$ ) and a significant interaction between treatment and TRP: $\Sigma$ LNAA ratios ( $F(1, 18) = 9.399$ ,  $p = .007$ ,  $\eta_p^2 = 0.343$ ). Impulsive choice on the delay-discounting task was increased after tryptophan depletion relative to placebo, to the

extent that tryptophan depletion reduced serotonin levels. There was a significant positive correlation between the magnitude of biochemical tryptophan depletion and the increase in impulsive choice on the discounting task after tryptophan depletion relative to placebo ( $r = .572$ ,  $p = .008$ ; Figure 2). That is, individuals showing the strongest biochemical response to the depletion procedure also showed larger increases in impulsive choice following the depletion procedure.

### Parallel Effects of Lowering Serotonin on Impulsive Choice and Altruistic Punishment

Previously, we reported that lowering serotonin in this sample increased altruistic punishment in the UG (Crockett et al., 2008). In this final analysis, we examined whether the effect of tryptophan depletion on impulsive choice in the delay-discounting task

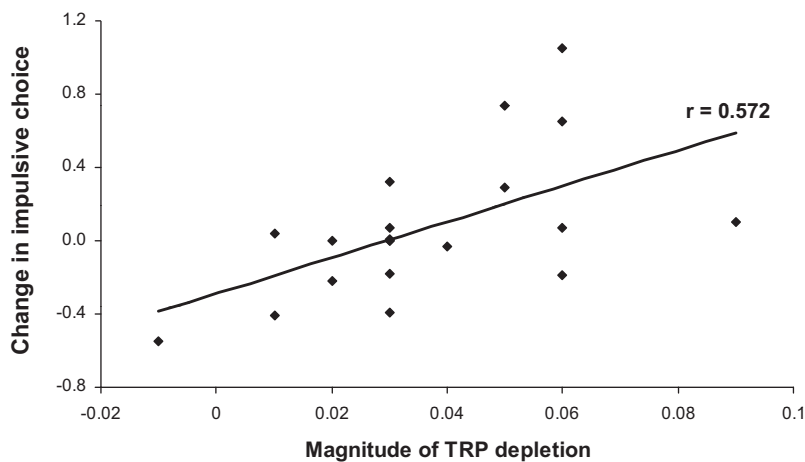


Figure 2. Reductions in plasma tryptophan (TRP) were significantly and positively correlated with increases in impulsive choice on the delay discounting task (log-transformed discount parameter) after tryptophan depletion,  $r = 0.572$ ,  $p = 0.008$ .

was correlated with the effect of tryptophan depletion on altruistic punishment in the UG. Across subjects, increases in impulsive choice resulting from tryptophan depletion were significantly and positively correlated with increases in rejection rates of unfair offers resulting from tryptophan depletion ( $r = .489, p = .021$ ; Figure 3), and increases in rejection rates of medium offers ( $r = .521, p = .013$ ) but not increases in rejection rates of fair offers ( $r = .256, p = .250$ ).

As impulsive choice was generally related to altruistic punishment across individuals, it is plausible that the discounting of delayed rewards represents an underlying process that plays a causal role in determining individual responses to unfair offers in the UG. That is, perhaps responders who reject a high proportion of unfair offers in the UG do so because they more strongly discount the *delayed* monetary benefits of accepting the offers relative to the *immediate* satisfaction of rejecting the offers. As lowering serotonin increased impulsive choice on the discounting task, one potential explanation for our finding that lowering serotonin increased altruistic punishment in the UG could be that increases in impulsive choice played a mediating role. To formally test the indirect effect of changes in impulsive choice after tryptophan depletion on changes in rejection rates of unfair offers after tryptophan depletion, we used the bias-corrected bootstrap method (with  $n = 1,000$  bootstrap resamples) as outlined in Preacher and Hayes (2008). This method does not assume a normal distribution of data and is recommended for small sample sizes (Shrout & Bolger, 2002). The true, indirect effect of depletion-induced changes in impulsive choice on unfair offer rejection rates was estimated to be between 0.1008 and 15.1921, with 95% confidence interval. Zero falls outside this confidence interval, supporting the conclusion that the indirect effect of changes in impulsive choice on unfair offer rejection rates is significantly different from zero ( $p < .05$ , two-tailed). These results indicate that depletion-induced increases in impulsive choice were significantly related to depletion-induced increases in altruistic punishment, independently from the effect of serotonin on both measures. In other words, serotonin depletion may shift preferences toward the *im-*

*mediate* satisfaction of punishing unfairness and away from the *delayed* monetary reward that results from accepting an offer.

## Discussion

Our results demonstrate that individual differences in impulsive choice predict altruistic punishment behavior in the UG. Preferences for small immediate rewards over larger delayed rewards were associated with a stronger tendency to punish proposers who made unfair offers. These findings contradict the idea that altruistic punishment in the UG is an exercise in self-control; if this were the case, we should have found the opposite relationship between individual differences in impulsive choice and individual differences in altruistic punishment behavior.

The fact that temporarily lowering serotonin increased both impulsive choice and altruistic punishment in the UG (Crockett et al., 2008) further supports our claim that altruistic punishment reflects the absence, rather than the presence of self-control. Moreover, the effects of lowering serotonin on impulsive choice and altruistic punishment were correlated across individuals, suggesting that common neural mechanisms underlie these processes. Although our measure of impulsive choice employed hypothetical as opposed to real monetary rewards, past research has shown that hypothetical monetary rewards are discounted in a similar manner to real monetary rewards (Johnson & Bickel, 2002; Madden, Begotka, Raiff, & Kastern, 2003).

Our findings imply that altruistic punishment behavior is an impulsive emotional reaction to perceived unfairness rather than a deliberative, goal-directed process. In line with this hypothesis, others have reported that responders are faster to reject than accept unfair offers (van't Wout, Kahn, Sanfey, & Aleman, 2005), and time pressure increases rejection rates in the UG (Sutter, Kocher, & Strauss, 2003). However, we do not mean to suggest that altruistic punishment is necessarily "irrational"; utility in the UG may well extend beyond the material value of the offers. Many studies support the view that punishing noncooperators is intrinsically rewarding. When responders' decisions impact only on

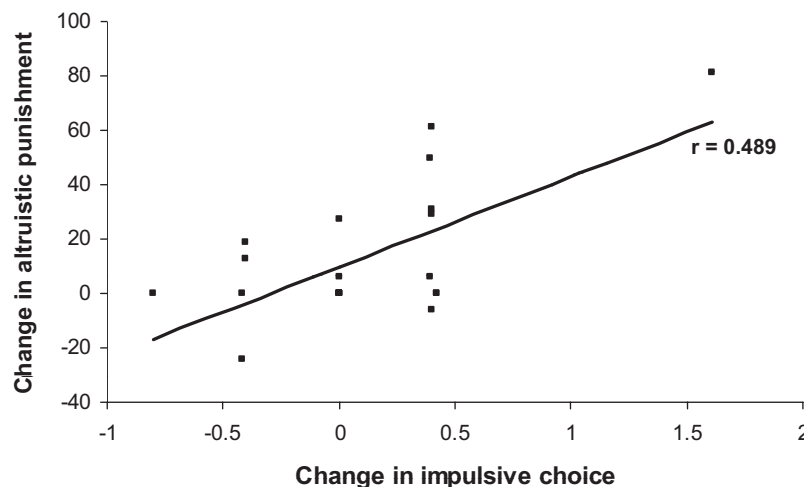


Figure 3. Increases in impulsive choice on the delay discounting task (log-transformed discount parameter) after tryptophan depletion were significantly and positively correlated with increases in costly punishment (percent of unfair offers rejected) after tryptophan depletion,  $r = 0.489, p = 0.021$ .

themselves (i.e., the proposer will be paid even if the responder rejects), responders almost never reject unfair offers (Bolton & Zwick, 1995). The dorsal striatum, a brain region implicated in instrumental reward anticipation (O'Doherty et al., 2004), is activated when people decide whether and how much to punish norm violators in the trust game; people with greater activity in this region are willing to incur higher personal costs to punish, suggesting that the dorsal striatum encodes the personal satisfaction derived from enforcing punishment (de Quervain et al., 2004). Furthermore, watching unfair players receive electric shocks activates the ventral striatum (Singer et al., 2006), a region implicated in passive reward prediction (O'Doherty et al., 2004); ventral striatal activity was positively correlated with expressed desire for revenge (Singer et al., 2006).

In most economic games used to study altruistic punishment behavior, the emotional satisfaction derived from punishing (e.g., rejecting an unfair offer) is immediate, while the monetary benefit of not punishing (e.g., accepting an unfair offer) is delayed until the end of the experiment. This suggests a potential mechanism underlying the relationship between serotonin depletion, impulsive choice and altruistic punishment: perhaps the tendency to engage in altruistic punishment arises from the tendency to favor immediate rewards over delayed rewards. This interpretation is bolstered by our finding that depletion-induced increases in impulsive choice had significant effects on altruistic punishment independent from the effects of serotonin depletion on altruistic punishment.

A plausible alternative explanation for the effects of serotonin depletion on impulsive choice and altruistic punishment concerns the hypothesis that serotonin is involved in assigning aversive value (Daw et al., 2002). According to this hypothesis, depleting serotonin could make the monetary losses resulting from rejecting offers seem less aversive, thus making rejection less 'costly.' However, we can rule out this explanation for the current data: in the same subjects, serotonin depletion had no effect on behavioral adjustment in line with punishment contingencies, indicating that serotonin is not critical for the assignment of aversive value (Crockett et al., 2009).

Impulsivity and self-control are complex multidimensional constructs, and the current study examined just one facet: impulsive choice, or preference for small immediate rewards over larger delayed rewards. This facet of impulsivity is highly relevant for the decision-making context of the UG (Reynolds et al., 2006), although we have not captured the entire construct of impulsivity with this measure. Some have even argued that this measure does not solely measure impulsive choice (Sozou, 1998); however, there is evidence that impulsive choice correlates with other varieties of impulsivity (Kirby & Finch, 2010), and has high ecological validity as a measure of self-control (Bickel et al., 2007; Petry, 2001; Reynolds, 2006; Weller, Cook, Avsar, & Cox, 2008). We did examine another facet of impulsivity in this sample of volunteers: motor impulsivity as measured by the Go/No-go task. We reported previously that serotonin depletion did not influence motor impulsivity, consistent with previous studies (Crockett et al., 2008); in addition, individual differences in motor impulsivity were not correlated with individual differences in altruistic punishment in the UG (M.J. Crockett, unpublished observations). This suggests that only certain aspects of impulsivity are relevant for altruistic punishment. Future studies might examine whether other aspects of impulsivity and self-control (e.g., risk-taking, future orientation) influence altruistic punishment, and under what circumstances.

Where does the impulse to punish unfairness originate? The existence of altruistic punishment in nonhuman species is controversial, but there is some evidence that primates punish noncooperative peers with retaliative aggression (Silk, 2005). The link between altruistic punishment and aggression is further supported by the fact that they share underlying neural mechanisms. Both aggressive responses to provocation and altruistic punishment of noncooperators are associated with activity in the medial prefrontal cortex (mPFC) (de Quervain et al., 2004; Lotze, Veit, Anders, & Birbaumer, 2007); and lowering serotonin increases both reactive aggression (Cleare & Bond, 1995) and altruistic punishment (Crockett et al., 2008).

Altruistic punishment is just one example of a behavior that promotes cooperation within groups— that is, a “prosocial” behavior. Notably, cooperation itself has also been linked to both impulsive choice and serotonin function in humans. In the repeated prisoner's dilemma, individuals who choose impulsively on the delay-discounting task are less likely to cooperate (Yi, Johnson, & Bickel, 2005); and lowering serotonin with tryptophan depletion reduces cooperation in the repeated prisoner's dilemma (Wood, Rilling, Sanfey, Bhagwagar, & Rogers, 2006). Comparing these findings to the present data, it appears that impulsive choice is positively correlated with one type of pro-social behavior (altruistic punishment in the UG), but negatively correlated with another type of pro-social behavior (cooperation in the prisoner's dilemma). This suggests that serotonin does not necessarily function to ensure group harmony, but is more related to impulsivity and aggression that are each capable of increasing or decreasing group harmony depending on conditions.

Taken together with other studies in this area, the current study highlights the complexity of the psychological and neural mechanisms underlying prosocial behavior in humans, and suggests that prosocial behavior may not be a unitary construct. Social norm adherence and enforcement may be governed by multiple independent neural systems: an abstract, rule-based system based in DLPFC, which represents fairness goals (Knoch et al., 2006); and a spiteful, emotion-driven system including the mPFC, insula and striatum, which represent the immediately reinforcing aspects of sanctioning norm violators (de Quervain et al., 2004; Koenigs & Tranel, 2007; Sanfey et al., 2003; Singer et al., 2006; Tabibnia et al., 2008). Environmental factors, such as food availability or chronic stress, may impact the functioning of these systems through their influence on the levels of neuromodulators like serotonin (Crockett, 2009). Defining the influence of neuromodulators on altruistic punishment may therefore enhance our understanding of how context shapes human social behavior.

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